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Weak environmental controls on the composition and diversity of medium and large-sized vertebrate assemblages in neotropical rain forests of the Guiana Shield

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Abstract

Aim: Despite their often high-trophic position and their contribution to many ecosystem functions, little is known about the factors affecting assemblage structure of medium- and large-sized neotropical vertebrates. We examined the relative roles played by the physical and biological environment, and by purely spatial processes, in shaping the composition and diversities of these vertebrate assemblages. Then, based on the theory that the Guianan forest cover shrank to isolated pockets during the late Pleistocene–Holocene, we tested if the past forest refugia may have shaped current vertebrate assemblages.

Location: French Guiana, Guiana Shield, South America.

Methods: Abundances of 19 medium- and large-sized vertebrates were estimated at 21 locations in undisturbed Guianan rain forests. Using taxonomic, functional and phylogenetic metrics, we partitioned the effects of a range of physical and biological environmental conditions and purely spatial predictors in shaping both assemblage composition and (alpha and beta) diversities.

Results: We identified a significant, but weak relationship between taxonomic, functional and phylogenetic assemblage composition and environmental conditions. Assemblage diversity patterns were mainly explained by spatial predictors irrespective of the metrics. Current assemblage diversities are correlated with Pleistocene–Holocene forest history, with the highest alpha diversities outside of putative forest refugia, and the highest beta diversities inside these areas.

Main conclusions: Current vertebrate assemblage composition is not strongly marked by common environmental factors. Our main conclusion is that assemblage composition results from individual species responses to the environment. Our findings also suggest that dispersal-related processes or more probably historical processes shape (alpha and beta) diversity patterns. In fact, forest fragmentation during Pleistocene–Holocene climate changes could have led to isolated vertebrate assemblages evolving into unique species assemblages creating the current high beta diversity inside refugia, whereas the lower habitat stability outside of refugia could have led to mixed assemblages in areas recolonized by forest vertebrates (current high alpha diversity outside of refugia).

KEYWORDS
biodiversity, birds, functional traits, mammals, refugia hypothesis, spatial patterns

1 | INTRODUCTION

To reduce human impact on ecosystems and to help policymakers to conserve remaining biodiversity, it is crucial to understand the ecological processes governing species assemblages (we define a species assemblage as a group of species that co-occur and potentially interact). In Neotropical rain forests, the research on species assemblages has mainly focused on trees (Fortunel, Paine, Fine, Kraft, & Baraloto, 2013; Hardy, Couteron, Munoz, Ramesh, & Pélissier, 2012; Kraft & Ackerly, 2010; Swenson, Enquist, Thompson, & Zimmerman, 2007) and, to a lesser extent, birds (Gómez, Bravo, Brumfield, Tello, & Cadena, 2010; Robinson, Brawn, & Robinson, 2000) and invertebrates (Lamarre, 2015; Mezger & Pfeiffer, 2011). Medium- and large-sized vertebrates (hereafter called large vertebrates) are largely understudied due to the high costs of sampling low-density populations. Because of this, deciphering the relative roles of the environment, both physical and biological, and purely spatial processes (such as dispersal and competition for space) in shaping vertebrate assemblages remains challenging.

Species composition and diversity, because they present complementary views on assemblage structure (Condit et al., 2002), are two commonly studied emergent properties in community ecology (Morin, 2011). With regard to these properties, most ecologists agree on the main structuring processes (dispersal limitation, environmental filtering, etc.) (Cornell & Harrison, 2014), but opinions about their relative importance vary. Regarding vertebrate assemblages, the most obvious model is that physical (e.g., temperature) and biological conditions (e.g., vegetation composition) directly influence animal populations as they provide habitat requirements and food resources (Badgley & Fox, 2000; Coblentz & Riitters, 2004). Some physical conditions (e.g., precipitation) can also be considered as indirect drivers as they strongly affect the biological conditions to which a species is exposed. In contrast, purely spatial effects are more often interpreted as legacies of historical processes (e.g., past environmental conditions; Barthe et al., 2017), or present dispersal-related processes (e.g., dispersal limitation or mass effect; Franklin et al., 2013). Ignoring space *per se* may therefore result in a failure to detect the underlying ecological processes at work (Cottenie, 2005; Dray et al., 2012).

Both assemblage composition and diversity may be assessed with various metrics (taxonomic, functional or phylogenetic) depending on the ecological process of interest. Taxonomic metrics can be used to identify hotspots and threatened assemblages in conservation planning (Margules & Pressey, 2000). However, they do not explicitly account for species' ecological differences. These can be assessed using both functional and phylogenetic metrics. Functional metrics capture the functional strategy within assemblages (de Bello et al., 2013; Luck, Lavorel, Mcintyre, & Lumb, 2012), and how these assemblages may respond to changes in environmental conditions. Incorporating functional traits allows us to define species assemblages in terms of resource acquisition, dispersal capacity and reproduction strategy (Cornwell, Schwilk, & Ackerly, 2006; Kraft et al., 2015; McGill, Enquist, Weiher, & Westoby, 2006). Functional metrics differ from phylogenetic metrics, as phylogenetic trees reflect evolutionary relationships alone, whereas functional trees also take into account functional convergence (Hérault, 2007). In this way, phylogenetic metrics incorporate a historical signal that can account for the relative importance of different clades in shaping species assemblages (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Graham & Fine, 2008). Furthermore, phylogenetic metrics can provide more integrated information than functional metrics which include only a limited number of easy-to-measure traits (Pavoine & Bonsall, 2011).

Because of their often high-trophic position, large vertebrate assemblages capture the cumulative effects of many basic ecosystem processes and their roles are important for the long-term maintenance of nutrient cycles, biomass, productivity and biodiversity of tropical rain forests (Dunham, 2008; Peres, Emilio, Schietti, Desmoulière, & Levi, 2016; Ripple et al., 2014; Terborgh et al., 2008; Wilkie, Bennett, Peres, & Cunningham, 2011). Geomorphology has emerged as the best environmental predictor of large vertebrate abundance, composition and diversity (taxonomic metrics) of Guianan *terra firme* (unflooded) rain forests (Denis et al., 2016; Richard-Hansen et al., 2015). Geomorphology probably keeps the traces of the ecological trajectory of rain forests at the geological scale (Guitet, Pélissier, Brunaux, Jaouen, & Sabatier, 2015), thereby representing physical, biological conditions and spatial effects at the same time.

Historical events (fire, habitat fragmentation, climate change, etc.), species dispersal limitation and even interspecific interactions (e.g., competition) may lead to purely spatial signal shaping species assemblage structure (Borcard, Legendre, Avois-Jaquet, & Tuomisto, 2004; Couteron & Ollier, 2005). The climatic history of South America, which experienced a series of rapid environmental changes during the Pleistocene–Holocene (20,000–2,000 year ago), was of primary importance to vertebrate assemblages (Haffer, 1970; Vuilleumier, 1971). In French Guiana, the location of past forest refugia was based on the in-depth works of de Granville (1982) (floristic characteristics) and Tardy (1998) (palaeoecological studies). Recent studies have increasingly been in favour of these putative refugia (Boisselier-Dubayle, Leblois, Samadi, Lambourdière, & Sarthou, 2010; Dutech, Maggia, Tardy, Joly, & Jarne, 2003; Noonan & Gaucher, 2005). The regions most affected by drier climatic phases would have evolved differently to each other according to the authors: stable rain forest, open forests, dry tropical forests or savannas.

In this study, we focused on assemblages of 19 large vertebrates from 21 sampling sites across undisturbed Guianan *terra firme* rain forests. We investigated the importance of (a) environmental conditions, especially biological conditions, on functional and/or phylogenetic composition, under the hypothesis that assemblage composition depends on functional traits related to biological resource acquisition, (b) spatial predictors on taxonomic diversity, if past disturbances outside of refugia randomly depleted assemblages without strongly modifying average functional and/or phylogenetic characteristics, and (c) spatial predictors, as surrogates of historical

events, on functional and/or phylogenetic diversity, if some assemblages maintained their functional and/or phylogenetic diversity over time (more stable ecosystem: refugia) while other assemblages were strongly depleted by past disturbances (outside of refugia).

2 | METHODS

2.1 | Study area

French Guiana (2°7′–5°44″ North, and 51°38′–54°35′ West), situated between Suriname and the Brazilian state of Amapa, represents ~85,000 km^2 of the eastern Guiana Shield. Altitude generally ranges between 0 and 200 m above sea level (mean 140 m) with a few peaks above 800 m. Annual rainfall ranges from 3,600 mm (north-east) to 2,000 mm (south and west). Mean annual temperature is of 25.7°C. The 21 sites used in all analyses are either located within protected areas, or far enough (at least 6 km) from roads, paths and other areas with human impact (e.g., settlements) to be considered as unaffected by recent hunting pressure, including from indigenous communities.

2.2 | Modelling species population abundance

Vertebrates were sampled based on visual counts of large vertebrates recorded with line transect protocol (Peres (1999), Denis et al. (2016) and field design details in Supporting Information Appendix S1). Species population abundance was estimated using the generalized distance sampling model of Chandler, Royle, and King (2011), which is an extension of the N-mixture models for repeated-count data. This model determines the detection probability (probability of detecting an observation), and the temporary immigration (probability of it being present in the sampling strip during the survey period) which allows study of open populations (large and mobile species). This hierarchical model allows inferences to be drawn about the number of groups per area unit. Species abundance (individuals/km^2) was obtained by multiplying the estimated number of groups either with the mean group size of the site (≥6 groups precisely counted), or with the mean group size of all studied sites (<6 groups precisely counted).

We used the data from 36 sites (Figure 1) to better estimate detection probability per species, and thus species abundance. Twenty-one of these sites were used for all other analyses in the study. The different species of the Tinamidae (great tinamou, *Tinamus major*, and other *Crypturellus* species) were grouped together as they are difficult to distinguish in the field. For convenience, we use only the term "species" hereafter to refer to Timanidae and species *sensu stricto*. Only data for species with at least 20 observations were retained to ensure a good degree of confidence in the detection probability estimates (Peres, 1999). Each site was treated as a single line transect, combining the data from the 3–4 individual 3-km transects. Each of these single line transects was replicated 12 times. The sampling

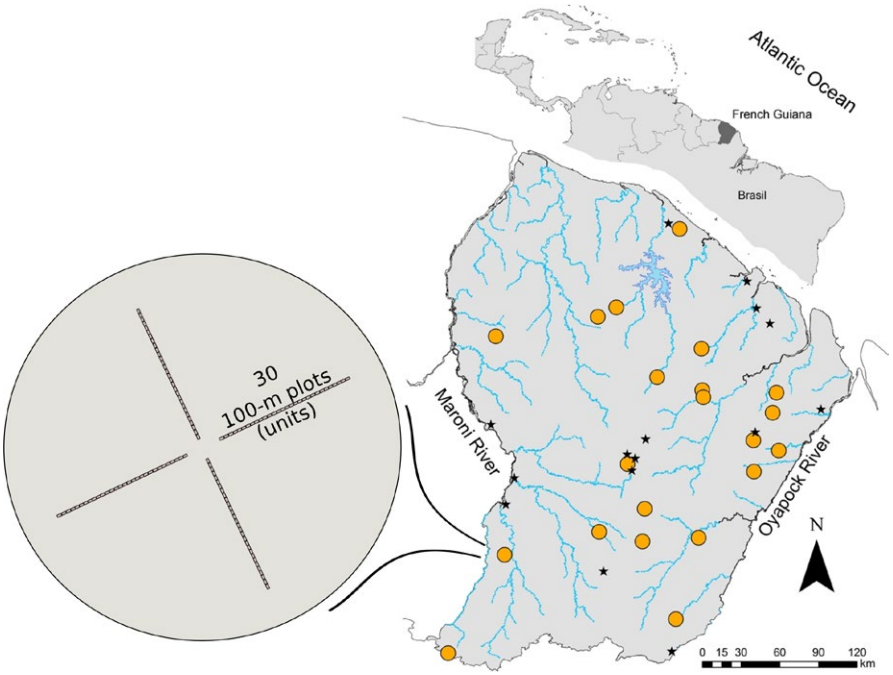

FIGURE 1 The study area in French Guiana, northern South America. Orange circles = sites used for all analyses, surveyed with line transects and described by remote sensing and field data; black stars = sites added to improve species density estimations, but not included in the partitioning analyses because of the unavailability of biological condition descriptors. The left part of the figure illustrates the sampling design: Four line transects were generally used to sample the diurnal large vertebrates (100 m transect unit), and biological conditions (i.e., forest structure and forest composition measured in each plot of 100 m × 20 m). Field data were aggregated to calculate environmental conditions at the site scale. For physical conditions, remote sensing data (Geographical Information System) were extracted within a 4-km radius from the centre of each site (grey disc) [Colour figure can be viewed at wileyonlinelibrary.com]

effort across sites varied from 60 to 191.7 km (mean 139.9 ± 23 *SD* km), which represents a total sampling effort of ~5,000 km. Only observations <50 m were included in the data set to exclude the least accurate distance estimates which avoid problems in fitting the detection function.

Each species' population density was estimated separately. Empirical Bayes methods were used to infer the intrinsic population abundance of each site (*ranef* R function). As data relating to variation in temporary immigration across sites were not available, we assumed that these movements were constant. To estimate detection probabilities, we used and compared the adjustment of half-normal or hazard-rate key functions according to Akaike information criterion (AIC) and chose the lowest (most parsimonious) model for each species. No covariate was included to calculate the detection probabilities as environmental conditions have a minimal influence on detectability in Guianan *terra firme* rain forests (Denis, Richardhansen, Brunaux, Guitet, & Hérault, 2017). Calculations were carried out using the R package *unmarked* (Fiske & Chandler, 2011).

2.3 | Physical and biological environmental conditions, and spatial covariates

2.3.1 | Physical conditions

All coarse-resolution descriptors were extracted from remote sensing data within a 4-km radius from the centre of each site (Figure 1 and Table 3). We used RAIN (annual rainfall) as the climatic descriptor. Topographical descriptors were obtained for each landform unit based on a recent geomorphological landform map generated from full-resolution Shuttle Radar Topography Mission (SRTM; 1 arc sec ~30 m) data. Then, at the site level, MSLO (mean slope of landforms), ELEV (mean elevation) and WET (mean wetness index i.e., proportion of hydromorphic areas) were averaged (Guitet et al., 2013).

2.3.2 | Biological conditions

For the biological conditions, all fine-resolution descriptors of forest structure and botanical composition were collected from 120 0.2 ha (100 × 20 m) quadrats on the 3–4 individual 3-km transects (left panel of Figure 1) over a period of 1 month before conducting species counts. TFG (Mean size of tree-fall gaps) was calculated to reflect the forest dynamic regime. EUT (density of *Euterpe* spp.) was used to represent swamp forests that are interspersed in the landscape. Five covariates were calculated from the dominant tree family abundance, which reflect tree beta diversity patterns across French Guiana at different spatial extents (Guitet, Pélissier, et al., 2015). LECY-CAES (abundance of Lecythidaceae and Caesalpinioideae; northwestern regional pattern), which was negatively correlated with BURS-MIMO (abundance of Burseraceae and Mimosoideae; southeastern regional pattern), LECY (abundance of Lecythidaceae; north-eastern subregional pattern) and CAES (Caesalpinioideae; eastern-southwestern-northwestern subregional patterns), which expressed tree dominance at intermediate spatial extents (<150 km), and CHR-SAP (abundance of Chrysobalanaceae and Sapotaceae) at local spatial extents (<10 km). TBA (tree basal area) was calculated and directly related to above-ground forest biomass (Guitet, Hérault, Molto, Brunaux, & Couteron, 2015). We also included THET (standard deviation of tree diameters) to estimate forest structure heterogeneity as a reflection of microhabitat diversity. Finally, ZOO (abundance of zoochorous trees) was obtained from a functional traits database (Ollivier, Baraloto, & Marcon, 2007) and van Roosmalen (1985)'s book, classifying a tree species as zoochorous if the genus or the family of the tree was known as strictly zoochorous. ZOO was used as proxy of food availability for frugivore/granivore species.

2.3.3 | Spatial covariates

We generated explicit predictors of the underlying spatial structure of our sampling points to be used in uni- and multivariate response analysis. For this, we applied distance-based Moran's eigenvector maps (dbMEMs; Borcard & Legendre, 2002; Dray et al., 2012) calculated from the geographical distances between site pairs. As spatial predictors, we used all the eigenvectors with positive eigenvalues, which model spatial structure at different scales with the first ranked spatial predictors representing the broadest spatial structure of the study area. All spatial predictors are orthogonal (i.e., uncorrelated with each other). Calculations were made with the R package *PCNM* (Legendre, Borcard, Blanchet, & Dray, 2013).

2.4 | Functional traits and phylogeny

Functional traits were chosen to their links to resource acquisition and dispersal capacity of vertebrate species. We used seven functional traits (Table 1). SIZE (body size), MASS (body mass), GRPSIZE (mean group size) and HR (size of home range) (which are relatively correlated) can be influenced by the quantity of resources available, and can impact ecosystem function, for example through seed dispersion. SIZE and MASS were correlated with extinction risk to identify the species most susceptible to extinction from particular disturbances (Fritz, Bininda-Emonds, & Purvis, 2009; Gaston & Blackburn, 1995). SIZE and MASS provide a considerable amount of other information (see Woodward et al., 2005; and list in Mokany et al., 2014). FRUITS (frugivory/granivory) or VEG (herbivory) as diet traits can be related to the quality of resources available (e.g., zoochorious trees abundance), or forest productivity (forest dynamics). HGT (height of substrate preference) can reflect how resource availability and strata (space) are exploited by species. Data were obtained from the literature from French Guiana when available, otherwise from elsewhere in South America (see Supporting Information Appendix S2).

As we did not have a dated phylogenetic tree, and given that Ricotta, Godefroid, Heathfield, and Mazzoleni (2013) showed that diversity calculated with dated phylogeny was highly correlated with diversity calculated from taxonomic classification trees, phylogeny was inferred from traditional taxonomic trees. We used the

following taxonomic levels to calculate phylogenetic distance between species: class, order, family and genus (order and family levels in Table 2), and to build phylogenetic trees: two species of the same genus have a distance of 1, two species of the same family have a distance of 2, etc. Functional and phylogenetic trees were built using R packages *stats* and *ade4* (Supporting Information Figure S3.1-2).

2.5 | Assemblage composition: Partitioning variance between environmental conditions and spatial predictors

Redundancy analyses (RDA) were implemented to assess the effects of environmental (physical and biological) conditions and spatial predictors (geographic distances) on the taxonomic, functional and

TABLE 1 Summary of functional trait covariates of large vertebrate species. The median value, the 5% and 95% quantiles (90% range) and the unit of measurement are given for each functional trait covariate. Height of substrate preference is an ordinal variable (terrestrial species and arboreal species using the lower (0) to upper levels (5) of forests)

Acronyms	Variables	Median	90% range	Units
Mass	Body mass	3.0	0.48–20.16	kg
Size	Body size	0.5	0.28–0.99	m
Hr	Size of home range	100.0	2.8–650	ha
GrpSize	Mean group size	2.0	1–14.6	individuals/group
Hgt	Height of substrate preference	0.0	0–4.1	–
Fruits	Frugivory/Granivory	68.3	24.6–97.51	%
Veg	Herbivory	1.0	0–36.85	%

TABLE2 Summary of species abundance in Guianan *terra firme* rain forests at 21 survey sites across French Guiana (Guiana Shield)

Order/family	Species	$D_{ind.}$	90% range	*SD*
Primates				
Atelidae	*Alouatta macconnelli*	6.21	3.76–14.37	3.93
	Ateles paniscus	3.24	0.89–6.88	2.23
Cebidae	*Sapajus [Cebus] apella*	11.77	2.37–22.72	6.13
	Cebus olivaceus	1.81	0.5–4.85	1.49
	Saguinus midas	4.60	1.03–9.63	2.89
	Saimiri sciureus	0.32	0.31–21.22	6.73
Pitheciidae	*Pithecia pithecia*	0.23	0.21–0.46	0.16
Artiodactyla				
Cervidae	*Mazama americana*	1.03	0.17–1.96	0.60
	Mazama nemorivaga	1.27	0.43–2.21	0.64
Tayassuidae	*Pecari tajacu*	2.80	1.92–4.94	1.73
Rodentia				
Dasyproctidae	*Dasyprocta leporina*	3.78	1.53–7.22	1.99
	Myoprocta acouchy	2.36	1.33–5.75	1.37
Carnivora				
Mustelidae	*Eira barbara*	0.63	0.56–0.66	0.04
Galliformes				
Cracidae	*Crax alector*	2.68	1.52–7.43	1.95
	Penelope marail	1.19	0.75–1.49	0.28
Gruiformes				
Odontophoridae	*Odontophorus gujanensis*	3.66	0.65–9.31	6.87
Psophiidae	*Psophia crepitans*	17.08	6.88–37.58	10.31
Tinamiformes				
Tinamidae	*Tinamidae*	11.83	4.98–20.72	5.09
Testudines				
Testudinidae	*Geochelone denticulata*	1.89	0.65–3.63	1.20

Note. $D_{ind.}$=median value of population density (individuals/km^2); 90% range=the 5% and 95% quantiles; *SD*=standard deviation.

phylogenetic composition of the assemblages. From among the 36 sites, we retained the 21 sites (orange circles on Figure 1) for which field environmental descriptors were available. We first created an abundance matrix by normalizing the raw population densities of each site (Supporting Information Table S4.1) to investigate assemblage composition independently of total species density. The abundance matrix was used as taxonomic composition matrix (top centre on Supporting Information Figure S5.1). The functional composition matrix (i.e., the average functional traits per site) was calculated by multiplying the abundance matrix with the trait matrix (Garnier et al., 2007) and the phylogenetic composition matrix was calculated by multiplying the abundance matrix with the phylogenetic distance matrix.

For each composition matrix, we ran a RDA which were constrained independently by each of the three covariate groups, that is the physical covariates, the biological covariates and the distance-based Moran's eigenvectors (spatial predictors). We then implemented a forward selection, based on the adjusted R^2, to reduce the number of covariates per RDA. Partial RDAs were then used to partition the assemblage variation explained by the three covariate groups (Peres-Neto, Legendre, Dray, & Borcard, 2006). The significance of covariate groups was assessed using a Monte-Carlo test (9,999 permutations). Multivariate analyses were conducted using the R packages *ade4* and *vegan* (Dray & Dufour, 2007; Oksanen et al., 2016).

2.6 | Taxonomic, functional and phylogenetic alpha and beta diversities

We used the Tsallis's generalized alpha entropy ${}^{q}H_{\alpha}$ to compute ${}^{q}_{i}H_{\alpha}$, the alpha entropy of the local assemblage *i*. Moreover, the entropy was then decomposed to calculate ${}^{q}_{i}H_{\beta}$, the contribution of a local assemblage *i* to the beta entropy (bottom centre on Supporting Information Figure S5.1; Marcon, Scotti, Hérault, Rossi, & Lang, 2014). Alpha and beta entropies were calculated for $q = 2$ (equivalent to the Simpson index) and were then transformed into equivalent numbers (Marcon & Hérault, 2015a) to get diversity indices. We incorporated traits-based and phylogeny-based trees (bottom left and right on Supporting Information Figure S5.1, respectively) to compute functional and phylogenetic alpha and beta entropies, and then corresponding diversity indices (Pavoine & Bonsall, 2011; Pavoine, Love, & Bonsall, 2009). Calculations were conducted using the R package *entropart* (Marcon & Hérault, 2015b).

Diversity indices were regressed against each of the three covariate groups using a Gaussian linear model. We then implemented a forward Akaike information criterion (AIC)-based selection, and partial multiple regressions were used to partition and test the variation explained by the three covariate groups (Peres-Neto et al., 2006). The effects of individual covariates were estimated using regression coefficients which were standardized due to multicollinearity among the covariates (Cade, 2015). Within this framework, the most important covariate has a value of 1.

Finally, we tested whether the putative forest refugia could explain the observed patterns of diversities. Refugia areas (darker green area of left panel of Figure 2a) were the consensus of the most probable areas defined by de Granville (1982) and Tardy (1998). Around these putative refugia, we designated four concentric buffer zones which included 5–6 sites each. We then carried out a Kruskal–Wallis test to assess whether alpha and beta diversities differed between the putative refugia and buffers.

3 | RESULTS

3.1 | Animal abundances

Animal abundance varied relatively strongly with respect to both species and sites (Table 2 and Supporting Information Table S4.1). In this study, the rarest species was the tayra (*Eira barbara*, Mustelidae) which is the least frugivorous/granivorous and herbivorous species (more carnivorous). The most common species was the grey-winged trumpeter (*Psophia crepitans*) with up to 38.3 ind./km^2. Physical and biological covariates were the most important covariates which

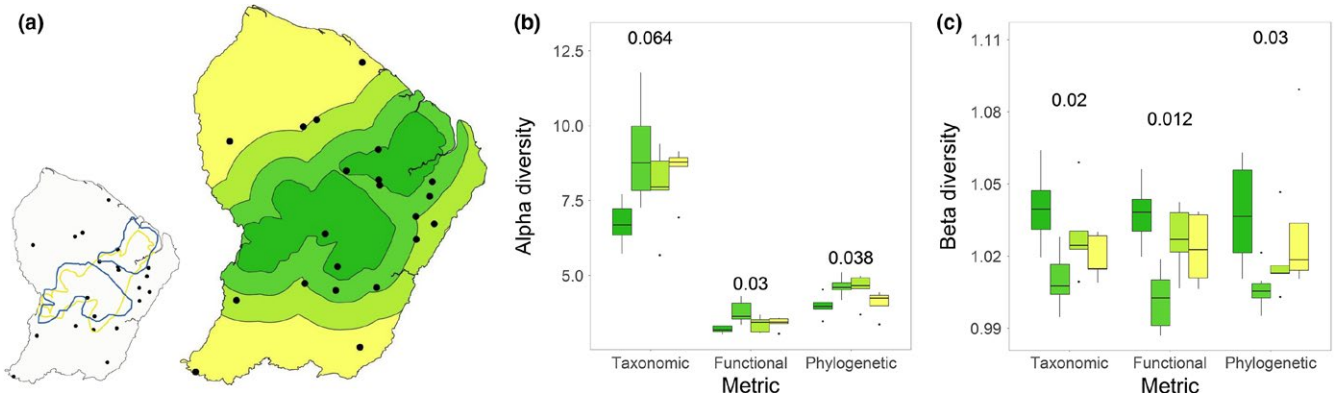

FIGURE 2 Difference in alpha and beta diversities between four rain forest areas buffers which are varying distances from putative refugia (central area in darker green). Central area was built from the works of de Granville (1982) and Tardy (1998) by intersecting the two areas that they considered as the most probable refugia (left panel). In right panels, box colour corresponds to those of four rain forest areas buffers. The *p*-value of the Kruskal–Wallis test is given above boxes [Colour figure can be viewed at wileyonlinelibrary.com]

affected individual species abundance for eight species while spatial predictors had lower effects. There was no single physical or biological covariate that strongly influenced a great number of species (method and results in Supporting Information Appendix S6).

Abundance variation (*SD* [standard deviation] column in Table 2) was lowest for tayra (*Eira Barbara*), red brocket (*Mazama americana*), Amazonian brown brocket deer (*Mazama nemorivaga*), Marail Guan (*Penelope marail*) and white-faced saki (*Pithecia pithecia*) which are solitary or live in small groups (family), and/or had a low variation in group abundance between sites. *SD* was highest for Guianan brown Capuchin (*Sapajus apella*), common squirrel monkey (*Saimiri sciureus*), marbled wood-quail (*Odontophorus gujanensis*), Tinamidae and the grey-winged trumpeter, which are species that live in groups and/or had high variation in group abundance between sites. Abundance variations of other species were relatively similar, with *SD*'s between 1.2 and 3.93.

3.2 | Assemblage diversity patterns

Alpha diversities were more variable than beta diversities. Taxonomic alpha diversity varied more strongly than functional and phylogenetic alpha diversities. Taxonomic, functional and phylogenetic beta diversities varied in similar ways (Supporting Information Table S4.2). For all the diversities, Figure 3a–f showed a high spatial aggregation. Alpha diversities were higher in the north-eastern French Guiana (Figure 3a–b and, to a lesser extent, c). Beta diversities were higher in the centre and south-west (Figure 3d–f).

3.3 | Covariate effects on assemblage composition

Biological conditions covariates differed among sites, and highlighted the environmental heterogeneity throughout French Guiana (Table 3 and Supporting Information Appendix S4). The selected covariates explained no more than a quarter of taxonomic composition variation (Adj.R^2 = 21.2%, p = 0.003, n = 9, 21 sites; Figure 4a) and did not explain the functional and phylogenetic metrics (Adj.R^2 = 7.1% and 8.8%, p = 0.24 and 0.10, n = 6 and 2, respectively; Supporting Information Figure S7.1). Taxonomic composition was best explained by environmental conditions (Adj.R^2 = 15%, p = 0.004), with physical and biological components having equivalent effects (Adj.R^2 = 10% and 10.7%, p = 0.005 and 0.002, respectively; Figure 4a). In fact, CHR-SAP (abundance of Chrysobalanaceae and Sapotaceae) was strongly correlated with the first RDA axis (r = 0.71), WET (mean wetness index) and MSLO (mean slope of landforms) were correlated with the second axis (r = 0.82 and −0.81, respectively; Figure 5a–b). On the first axis, the species mostly positively related to the CHR-SAP were the Tinamidae species, marail guan, white-faced saki and collared peccary (*Pecari tajacu*), all of which have diets that consist of >60% fruit. On the second axis, common squirrel monkey and red-rumped agouti (*Dasyprocta leporina*) were negatively related to WET, and negatively related to MSLO. Guianan red howler monkey (*Alouatta macconnelli*) and black curassow (*Crax alector*) were negatively related to WET and positively related to MSLO.

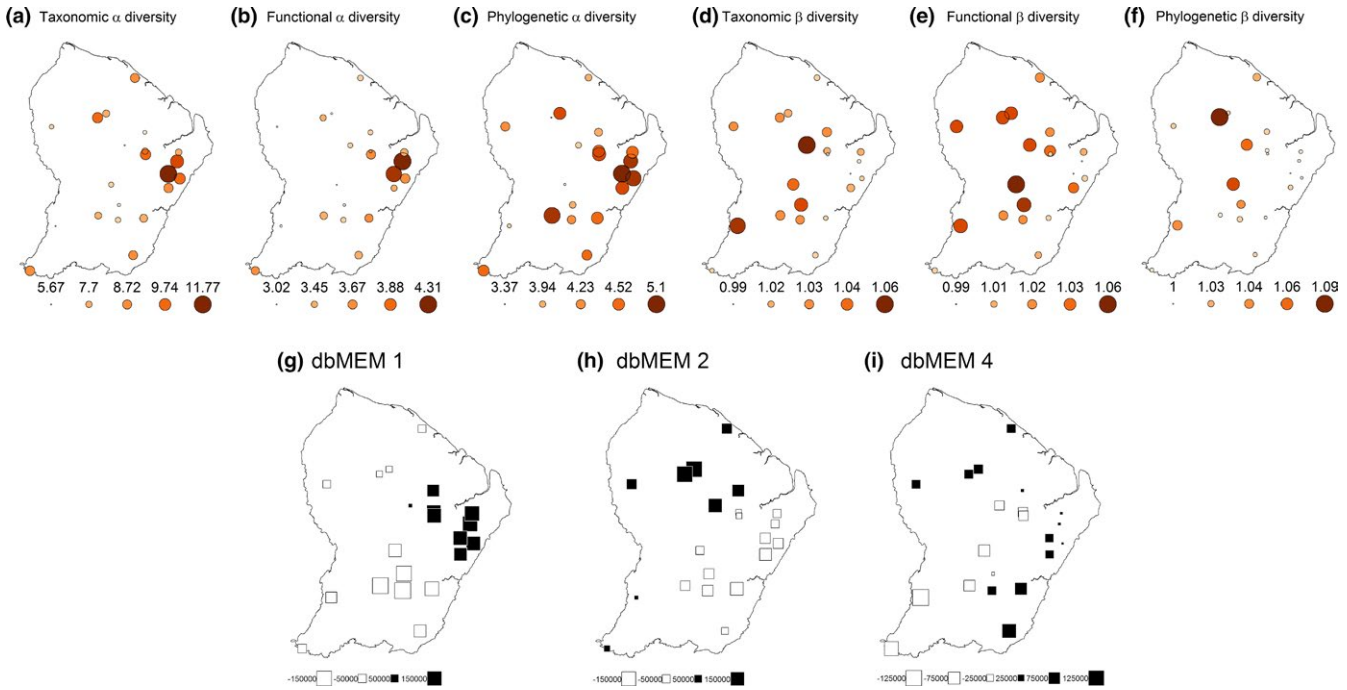

FIGURE 3 Observed spatial patterns of alpha and beta diversities related to spatial predictors across French Guiana. In the first line, a–f represent the spatial patterns of observed alpha and beta diversities at survey sites. In the second line, g–i illustrate the three more significant spatial predictors (dbMEMs: distance-based Moran's eigenvectors) selected and used to predict alpha and beta diversities (see pattern similarities with a–f). Square size is proportional to values of spatial predictors (where negative values are in white and positive values are in black) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Summary of biological and physical condition covariates that potentially influence large vertebrates. The median value, the 5% and 95% quantiles (90% range), CV (coefficient of variation) and the unit of measurement are given. The last column is the results of one-way ANOVA to test biological conditions differences between sites $F_{(DF_F,DF_E)} = SS_F/SS_E$, where DF_F and DF_E are the number of degree of freedom for the factor and error terms, respectively. MS_F and MS_E are the variation mean between group (factor) and variation mean within groups, respectively (MS: mean squares)

Acronyms	Variables	Median	90% range	CV	Units	ANOVA tests
a – Biological covariates						
Zoo	Density of zoochorious trees/palms	124.28	79.63–141.73	0.19	Stem/ha	$F_{(20,2393)} = 2,422.1/131.3 = 18.4$; $p < 0.001$
THet	Tree diameter heterogeneity	19.11	17.34–21.74	0.09	m^2	$F_{(20,2393)} = 224.9/12.2 = 18.4$; $p < 0.001$
Tba	Tree basal area	23.47	20.41–26.24	0.1	m^2/ha	$F_{(20,2385)} = 623.6/44.7 = 13.9$; $p < 0.001$
Lecy-Caes	Lecythidaceae and Caesalpinioideae	49.55	18.38–73.87	0.44	Stem/ha	$F_{(20,2393)} = 2,078.1/30.1 = 69$; $p < 0.001$
Burs-Mimo	Burseraceae and Mimosoideae	3.57	3.16–3.94	0.09	Stem/ha	$F_{(20,2393)} = 783.3/13.4 = 58.5$; $p < 0.001$
Lecy	Lecythidaceae	3	2.05–3.75	0.19	Stem/ha	$F_{(20,2393)} = 669.9/12.8 = 52.1$; $p < 0.001$
Caes	Caesalpinioideae	24.27	6.44–44.19	0.5	Stem/ha	$F_{(20,2393)} = 730.2/17.2 = 42.4$; $p < 0.001$
Chryso-Sapo	Chrysobalanaceae and Sapotaceae	28.53	8.59–67.72	0.52	Stem/ha	$F_{(20,2393)} = 1,534.5/19.6 = 78.4$; $p < 0.001$
Eut	Euterpe spp. density	26.28	5.16–102.65	0.94	Stem/ha	$F_{(20,2393)} = 152,672.9/25,735.4 = 5.9$; $p < 0.001$
Tfg	Mean size of tree-fall gaps	152.08	63.33–302.29	0.51	m^2	$F_{(20,2385)} = 794,237.2/168,740.9 = 4.7$; $p < 0.001$
b – Physical covariates						
MSlo	Mean slope of landforms	14.6	7.1–21.5	0.3	°	
Wet	Mean wetness index	28	20–48	0.31	%	
Elev	Mean elevation	139.79	55.12–372.37	0.63	m	
Rain	Annual rainfall	2,700	2,300–3,400	0.13	mm	

3.4 | Covariate effects on assemblage diversities

3.4.1 | Alpha diversity

In contrast to composition, the selected covariates explained a significant part of variation in alpha diversity, particularly for the phylogenetic metric (Adj.R^2 = 35.5%, p = 0.006, n = 4, 21 sites; Figure 4b), with close values for the taxonomic and functional metrics (Adj.R^2 = 28.4% and 26%, p = 0.01 and 0.03, n = 3 and 4, respectively; Supporting Information Figure S7.1). The spatial predictors had the highest explanatory power (Adj.R^2 = 28.4%–35.3%), whereas the effects of environmental (physical and biological) conditions were lowest (Adj.R^2 = 11.5%–15.3%). dbMEM 1 and dbMEM 2 were always selected by the stepwise procedures (Table 4), and the relative importance of dbMEM 1 and dbMEM 2 was high (0.67–1).

3.4.2 | Beta diversity

Similarly to alpha diversity, the selected covariates explained a significant proportion of the variation in beta diversity, for the phylogenetic (Adj.R^2 = 36.1, p = 0.002, n = 3, 21 sites; Figure 4c), taxonomic and functional metrics (Adj.R^2 = 35.3% and 34.6%, p = 0.003 and 0.007, n = 3 and 4, respectively; Supporting Information Figure S7.1). The spatial predictors, dbMEM 1 and dbMEM 2, were the most important covariates for the phylogenetic (Adj.R^2 = 36.1%, p = 0.01), taxonomic (Adj.R^2 = 35.3%, p = 0.002) and functional (Adj.R^2 = 36.8%, p = 0.008) metrics. Physical and biological conditions had no or little effect irrespective of the metrics: taxonomic (no effect), functional (Adj.R^2 = 8%, p = 0.028) and phylogenetic (no effect).

3.4.3 | Spatial patterns of diversities

For both alpha and beta diversities, the largest (dbMEM 1 and dbMEM 2) spatial covariates are the best predictors (Table 4), with similar effects irrespective of the metrics (same signs of model-averaged parameter estimates; Table 4). Thus, effects of spatial predictors (dbMEM 1, dbMEM 2 and dbMEM 4 to a lesser extent) reveal that diversities are strongly spatially structured, but not by the effects of environmental conditions. Autocorrelation tests on spatial covariates dbMEM 1 and dbMEM 2 showed that sites that are within a 0–80 km distance of each other are more likely to have more similar diversity than sites that are 80–250 km apart (method

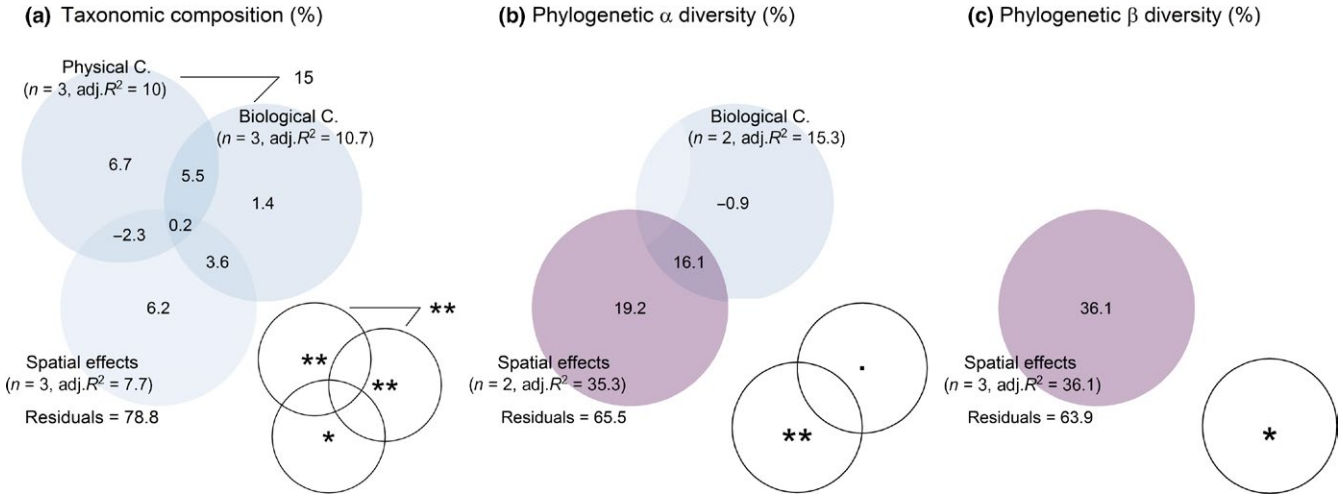

FIGURE 4 Variation partitioning Venn diagrams representing the contribution of physical, biological and spatial predictors to the large vertebrate assemblages at 21 sites across French Guiana for the taxonomic composition, phylogenetic alpha and beta diversities. In the larger figures (top left), fractions within circles depict the adjusted percentages of the pure and shared effects of covariate groups; values in brackets under covariate group name represent the number of selected covariates by groups (n) and the total variation (pure and shared) explained by the covariate group (%); colour circles are proportional to total variation in each covariate group (from white to violet); the value indicated by the two segments represents the total variation in physical and biological conditions, that is, environmental conditions; residuals represent the unexplained portion of variation; a circle is not represented if no covariate of a group was selected. In the smaller figure (bottom right), the statistical significance levels are indicated for separate pure and shared effects of biological conditions, physical conditions and spatial predictors: ** $p < 0.010$; * $p < 0.050$; $p < 0.100$ and NS = not significant [Colour figure can be viewed at wileyonlinelibrary.com]

and results on Supporting Information Figure S8.1). These two large spatial covariates worked together geographically to delimit the putative forest refugia, so that differences in alpha and beta diversities between the putative refugia and buffers were significant (*p*-values on Figure 2), with alpha diversities lower and beta diversities higher within refugia than in more remote areas.

4 | DISCUSSION

4.1 | Current environment slightly shapes large vertebrate assemblage composition

Our study highlights weak dependencies of assemblage composition on environmental (both physical and biological) conditions, with cumulative effects being of the same order of magnitude as previous results on simple geomorphology-based landscape classification (~25%; Richard-Hansen et al., 2015). Physical conditions are often seen as the primary ecological requirements of vertebrate assemblages. In our specific case, no particular functional trait or phylogenetic clade appears to be related to physical conditions (Figure 5). This suggests that environmental filters do not strongly shape the functional or phylogenetic structure of the studied vertebrate assemblages (Kleyer et al., 2012). In fact, the range of physical (e.g., soil, climate) conditions is probably not high enough to strongly affect Guianan vertebrate assemblages as a whole (Guitet et al., 2013).

With respect to biological conditions, abundance of Chrysobalanaceae and Sapotaceae were the best predictors of large vertebrate assemblage composition (Figure 5). These two families encompass the most common trees species in the area and represent on average a third of zoochorous species across sites (mean ± *SD*: 30.2% ± 15.4%). Large variations in the abundance of Chrysobalanaceae and Sapotaceae make these two families important foraging resources which potentially shape animal population distribution for several species (see Results). However, functional metrics failed to find relationships between diet (frugivory/granivory) traits and density of zoochorious trees/palms (Figure 5d-e). Furthermore, the phylogenetic metric predicts assemblage composition poorly, suggesting that phylogenetically close species may have different biological requirements in spite of this closeness. Some authors explain that the influence of fruit availability can be substantially different among closely related species such as primates (Carretero-Pinzón, Defler, McAlpine, & Rhodes, 2017; Stevenson, Quinones, & Ahumada, 2000). Phylogenetically distant species (e.g., a bird and a mammal) can be functionally similar (functional tree in Supporting Information Figure S3.1a).

The apparent low predictability of the functional and phylogenetic indices could be due to biotic interactions such as competition, which causes overdispersion in functional or phylogenetic space, and may thus hide environmental filtering. However, competition is often seen as a local (and not regional) predictor of community assemblage (Cavender-Bares et al., 2009). Alternative explanations are (a) the predominance of stochastic, that is neutral processes (e.g., local colonization/extinction) or (b) the results of individual species responses to environmental conditions (see Animal abundances subsection and similar results for small mammal assemblages in Pardini, Marques de Souza, Braga-Neto, & Metzger, 2005).

Although a wide range of environmental conditions was measured, the variation could be caused by unmeasured environmental

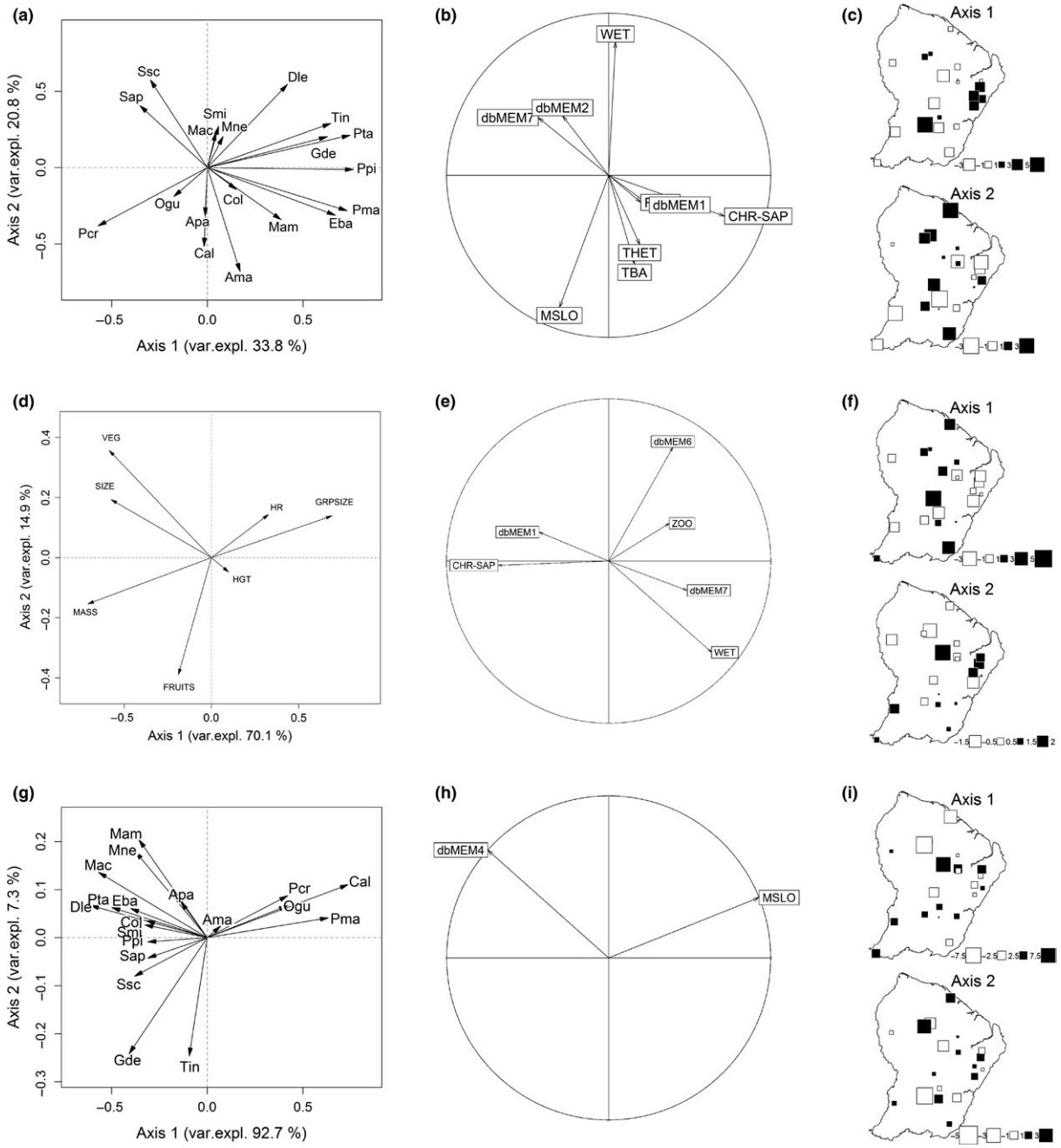

FIGURE 5 Results of the pRDA analysis carried out to highlight effects of environmental conditions on composition structure of large vertebrate assemblages using the taxonomic, functional and phylogenetic metrics. The covariate effects were illustrated on the first line (a-c) for taxonomic composition, on the second line (d-f) for functional composition, and on the third line (g-i) for phylogenetic composition. For the three metrics, left panels are the projections of species on pRDA factorial plan 1 and 2; central panels are the correlation circles for the first two axes of pRDA performed on the species abundance table with respect to selected environmental explanatory covariates; right panels are the plot scores along axes 1 and 2, projected on French Guiana maps: squares size is proportional to site scores (where negative values are in white and positive values are in black). Ama: *Alouatta macconnelli* (Linnaeus, 1766); Apa: *Ateles paniscus* (Linnaeus, 1758); Cal: *Crax alector* (Linnaeus, 1766); Col: *Cebus olivaceus* (Schomburgk, 1848); Dle: *Dasyprocta leporina* (Linnaeus, 1758); Eba: *Eira barbara* (Linnaeus, 1758); Gde: *Geochelone denticulata* (Linnaeus, 1766); Man: *Mazama americana* (Erxleben, 1777); Mne: *Mazama nemorivaga* (F. Cuvier, 1817); Mac: *Myoprocta acouchy* (Erxleben, 1777); Ogu: *Odontophorus gujanensis* (Gmelin, 1789); Pcr: *Psophia crepitans* (Linnaeus, 1758); Pma: *Penelope marail* (Müller, 1776); Ppi: *Pithecia pithecia* (Linnaeus, 1766); Pta: *Pecari tajacu* (Linnaeus, 1758); Sap: *Sapajus [Cebus] apella* (Linnaeus, 1758); Smi: *Saguinus midas* (Linnaeus, 1758); Ssc: *Saimiri sciureus* (Linnaeus, 1758); Tin: Tinamidae. EUT: *Euterpe* spp. density; TBA: tree basal area; CHR-SAP: abundance of Chrysobalanaceae and Sapotaceae; MSLO: mean slope of landforms; WET: mean wetness index; RAIN: annual rainfall; THET: Tree diameter heterogeneity; CAES: abundance of Caesalpiniaceae; LECY: abundance of Lecythidaceae. MASS: Body mass; SIZE: Body size; HR: Size of home range; SOCIAL: Social structure size; GRPSIZE: Mean group size; CALLS: Calls/Songs; HGT: Height of substrate preference; FRUITS: Frugivory/Granivory; VEG: Herbivory

TABLE 4 Results of covariate selection procedures for the taxonomic (Taxo), functional (Funct) and phylogenetic (Phylo) metrics. The covariates marked in the "composition" column indicate that they were selected (Figure 5 for covariate contribution to the first 2 pRDA axes). In the "diversity" column, the signs (+ or −) indicate covariate effects (positive or negative) and values in brackets are the ratios of parameter estimates for standardized predictors (based on partial standard deviations) that represent the relative importance of individual predictors (Cade, 2015)

	Composition			Diversity					
				α			β		
	Taxo	Funct	Phylo	Taxo	Funct	Phylo	Taxo	Funct	Phylo
Biological conditions									
Density of zoochorious trees/palms		✓				−(0.04)			
Tree diameter heterogeneity	✓								
Tree basal area	✓								
Lecythidaceae and Caesalpinioideae									
Burseraceae and Mimosoideae									
Lecythidaceae									
Caesalpinioideae									
Chrysobalanaceae and Sapotaceae	✓	✓			+(0.25)	+(0.26)			
Euterpe spp. density									
Mean size of tree-fall gaps									
Physical conditions									
Mean slope of landforms	✓		✓						
Mean wetness index	✓	✓							
Mean elevation									
Annual rainfall	✓				+(0.18)			−(0.17)	
Spatial covariates									
dbMEM 1	✓	✓		+(1)	+(1)	+ (0.67)	− (1)	− (0.99)	− (1)
dbMEM 2	✓			−(0.21)	−(0.8)	− (1)	+ (0.48)	+ (1)	+ (0.81)
dbMEM 3									− (0.3)
dbMEM 4			✓	+ (0.52)			− (0.84)		
dbMEM 5									
dbMEM 6		✓						− (0.4)	
dbMEM 7	✓	✓							

or spatial variables (Borcard et al., 2004). The lack of correlation could also be due to unmeasured and more pertinent functional traits (e.g., longevity, age of maturity, fecundity, dentition, dispersal distance, etc.) even though they probably add limited new information as they look redundant to the traits we considered (e.g., body size, diet traits Bennett & Owens, 1997; Mokany et al., 2014).

4.2 | Physical and biological conditions fail to explain diversities

Environmental parameters do not influence the diversity, which is in sharp contrast to numerous studies of, for example, tropical ants or tree communities in Borneo (Mezger & Pfeiffer, 2011; Slik et al., 2009). Our results showed no relationships between alpha diversities and the amount of resources (e.g., density of zoochorious trees/palms and *Euterpe* spp. palm), and habitat productivity (e.g., biomass), irrespective of metrics. However, our results contrast with recent findings showing that tree biomass (and carbon concentration in soil) could be linked to mammal richness, supporting the idea that assemblage complexity drives tropical ecosystem functioning through carbon retention (Sobral et al., 2017). Indeed, regularity (a component of alpha diversity) should be positively correlated with total ecosystem biomass, because of increasing complexity and better use of resources (Cavender-Bares et al., 2009; Mouillot, Mason, Dumay, & Wilson, 2005 for phylogenetic metric).

Regarding results on habitat heterogeneity, neither tree diameter heterogeneity nor mean size of tree-fall gap could be used as a proxy of habitat dynamics. Structurally complex habitats are predicted to support more complex and diverse assemblages, and thus increase species diversity (Mcclain & Barry, 2010; Tews et al., 2004). The majority of studies find a positive correlation between habitat heterogeneity (diversity) and animal species diversity (richness and alpha diversity). However, positive results are often overrepresented in publications in comparison with negative and null results (Tews et al., 2004).

4.3 | Hypotheses to explain spatially structured diversities

Because diversity patterns were mainly explained by spatial predictors, the role of neutral processes such as dispersal is probably more important than deterministic processes due to environmental conditions. Broad structural patterns may emerge when dispersal is limited either by low dispersal capacity or due to geographical barriers. Large vertebrates should disperse over large distances in the continuous forest cover of the Guiana Shield unless large rivers limit their movements. Large rivers in Guyana and Brazilian Amazonia were assumed to be barriers (Haugaasen & Peres, 2005; Lehman, 2004) but are less likely to be so in French Guiana where rivers are not so large (except some in the downstream sections of northern French Guiana).

Historical processes such as climate change-induced fragmentation of the forest (refugia hypothesis) could also explain French Guiana's largely spatial driven diversity patterns (Condit et al., 2002) on the broad scale. In addition to climate change, several long drought-associated fire events in the Holocene have been recorded in French Guiana (Charles-dominique et al., 1998; Tardy, 1998). Putative refugia were located in the higher elevations of northern and central French Guiana and have already been shown to shape taxonomic and allelic diversities (Boisselier-Dubayle et al., 2010; Dutech et al., 2003; Noonan & Gaucher, 2005). Historic isolation and/or habitat stability can influence assemblage diversity between regions (Guitet et al., 2018; Leprieur et al., 2011). Habitat fragmentation caused by climate change during the Pleistocene–Holocene could have played a key role in differences of diversity inside or outside of refugia. Disturbance intensity could have been heterogeneously spatially distributed, leading to isolated vertebrate assemblages evolving into unique species assemblages in more stable habitats, which translates today into high beta diversity values inside refugia (Figure 3d–f). Outside of refugia, past disturbances (successive phases of forest regression and recolonization) could have reduced habitat stability. This lower habitat stability could have lead to mixed assemblages in areas recolonized by forest vertebrates from undisturbed refugia, assemblages that are currently richer and more diverse (high alpha diversity values) than those of the refugia themselves (Figure 2b–c).

Our results show that differences in alpha and beta diversities result only from location, either within or without former refugia. These diversity patterns, combined with the weaker effects on functional and phylogenetic assemblages diversities, support the conclusion that neither geographical barriers nor environmental filters have strongly shaped vertebrate assemblages and confirm our findings concerning assemblage composition.

Our results highlight the fact that different spatial arrangement of conservation effort could result from the choice of conservation planning metrics and the statement of conservation planning objectives. The stark spatial disjunction between areas of high alpha and beta diversity highlights how priorities set using raw species abundance alone could be very different depending on the assemblage properties applied, and may relate not at all to priorities based on the distributions of the rarest or most threatened species.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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